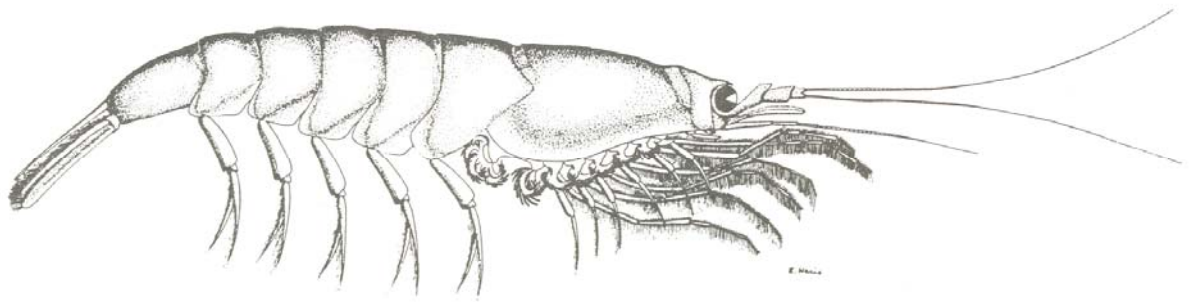


**Graduate Certificate in Antarctic Studies 2007: Review**

# **The Trophic Significance of Krill in the Southern Ocean Ecosystem**



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## Introduction

The Southern Ocean is a highly productive ecosystem that supports large populations of whales, seals, birds and fish and plankton. It is also one of the largest marine ecosystems on earth, covering approximately 36 million km<sup>2</sup>, bounded by the Antarctic Convergence to the north (Bathmann et al 2000).

Supporting the 30 million year old Antarctic marine ecosystem is the small but abundant Antarctic krill, or *Euphausia superba* as it is known scientifically (Major 1985). Krill are a key component of the diet of baleen whales, seals, penguins, petrels, terns, albatrosses, squid and many fish species (Major 1985). Antarctic krill are commonly found between the Antarctic coast and the edge of the pack ice but are also found north as far as the 59°S (Everson 1977).

Since the early 1920s, increasing efforts have been made to learn more about this cryptic species and its significance in the Antarctic ecosystem (Siegel 2005). Research initiatives such as the First and Second International BIOMASS Experiments (FIBEX and SIBEX) have focussed on biology, ecology and population dynamics of krill (Miller and Hampton 1989). Studies such as these have provided information on krill and the functioning of the Southern Ocean food web, yet there are still many gaps in our knowledge of krill life histories and trophic interactions due to the difficult logistics of conducting research in the Southern Ocean. In order to gain critical life history information on Antarctic krill it is necessary for scientists to compete with extreme weather and cover large areas of the Southern Ocean surrounding Antarctica which makes research difficult. Quantitative data on the biomass of krill, larval recruitment into the population and information on the trophic relationships of krill in the southern ocean food web are required before a proper understanding of population dynamics can be achieved. Anthropogenic impacts on the krill population also need to be examined in order to identify interactions within the ecosystem and manage the krill resource appropriately. The purpose of this review is to provide an overview of the biology and physiology of Antarctic krill, while presenting a synthesis of current knowledge on krill populations and their trophic significance in the Southern Ocean ecosystem.

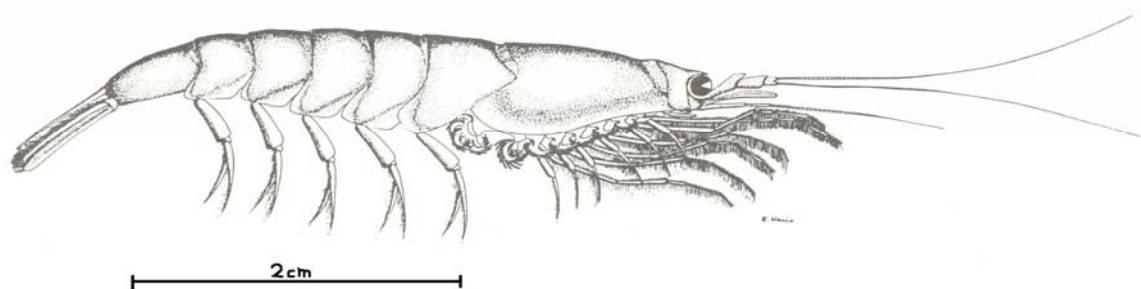
The role of krill in biogeochemical cycling, specifically the Biological Carbon Pump will also be identified and potential implications of commercial krill harvesting will be discussed.

## The Biology of Krill

The Southern Ocean surrounding Antarctica is home to a number of species of euphausiid crustaceans, of which *Euphausia superba* (Antarctic krill) is the largest and most abundant (Everson 1977). It is estimated that Antarctic krill account for 50% of the Antarctic zooplankton biomass (Gulland in Kirkwood 1982).

Krill are pelagic crustaceans that congregate in huge swarms during the summer months in the seas surrounding Antarctica (Nicol and de la Mare 1993). Of the 85 known species of Euphausiid, Antarctic krill (Fig. 1) are one of the largest species in the world, growing up to 70 mm in length (Miller and Hampton 1989). Krill are usually found in the top 200m of the water column (Everson 1977) and are identifiable by their two antennae, two large black eyes and five pairs of legs (Fig. 1), which are used for propulsion to maintain position in the water column and as food strainers (Major 1985).

Mature krill are the primary herbivore in the ocean surrounding Antarctica but they will also consume planktonic animals (zooplankton) depending on food availability (Siegfried et al 1985). Krill larvae in turn are also consumed by some carnivorous zooplankton species (Kirkwood 1982). The main predators of Antarctic krill are Cetaceans such as the baleen whales, birds, fish, squid and seals (Miller and Hampton 1989).



**Fig.1** Antarctic Krill, *Euphausia superba* at maturity (source: Major 1985:22)

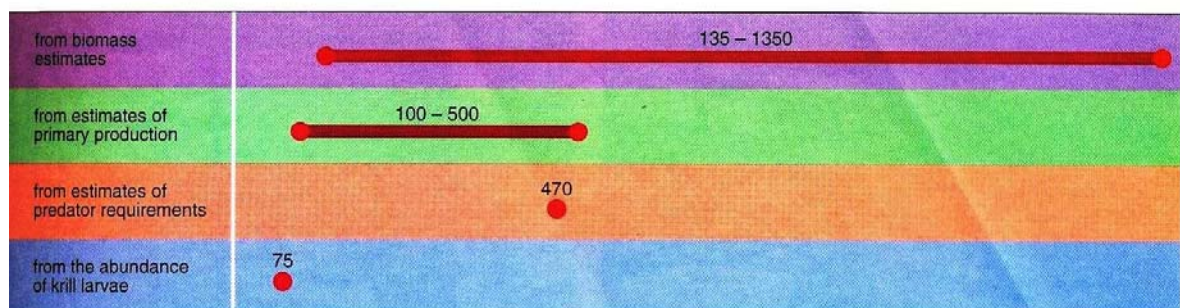
Krill spawn from January to March when the female lays several thousand eggs (Everson 1977). The eggs are less than 1mm in diameter and are released near the

surface before sinking to the seafloor where they hatch and begin to develop (Everson 1977). As the eggs develop through their larval stages they rise back up through the water column until they reach the surface, where they spend the spring months feeding on phytoplankton and ice algae at the ice edge and undergo further development into adolescents (Major 1985). It is thought to take two or more years for krill to reach maturity and grow to their maximum length of about 6cm (Everson 1977). Studies are continuing on the lifespan of krill in the wild, but lab specimens have survived for up to 9 years (Nicol and de la Mare 1993).

Another notable adaptation of krill is an ability to moult and revert to a juvenile form when subjected to long periods without food (Nicol and de la Mare 1993). Krill have been starved in a laboratory setting for up to 200 days and have been shown to metabolise their structural proteins and ‘shrink’ in size (Nicol and de la Mare 1993). For this reason, it has been difficult for scientists to apply a uniform aging method to krill based on size.

## Population Dynamics in the Southern Ocean

There have been many estimations of the size and strength of recruitment of the krill resource. Annual productivity (Fig. 2), has been estimated directly by measuring krill using acoustic surveys and trawl nets, and indirectly, by extrapolating biomass from predation and consumption rates (Miller and Hampton 1989). Although estimates of krill productivity between studies have been highly variable, the yearly production of krill is thought to be more than the total annual global catch of all marine species, which is over 99 million tons (Nicol and de la Mare 1993).

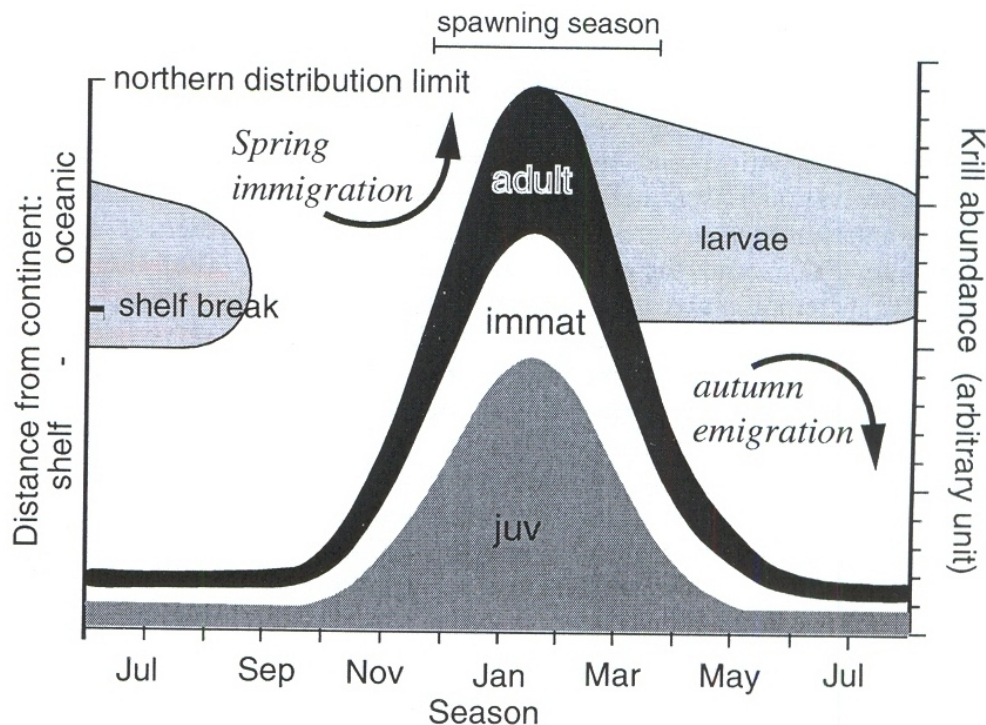


**Fig.2** Estimates of annual krill production in millions of metric tons (source: Nicol and de la Mare 1993:43)

Estimates of annual krill production range from 75 million tons to 1.35 billion tons (Fig. 2), while indirect estimates of the krill standing stock range from 14 million to 7 billion tons (Miller and Hampton 1989).

There are many variations in estimates of krill biomass because of gaps in the life history data of krill covering elements such as distribution, abundance and winter dispersal. Areas such as the Bellingshausen, Amundsen and Weddell Seas present a particular problem for researchers, as they are difficult to access and bound by ice for long periods (Siegel 2005).

Seasonal abundance and density of krill around the peninsula region has varied considerably, with low abundance over the continental shelf during winter and high abundance extending north as far as 59°S during the summer (Fig. 3).



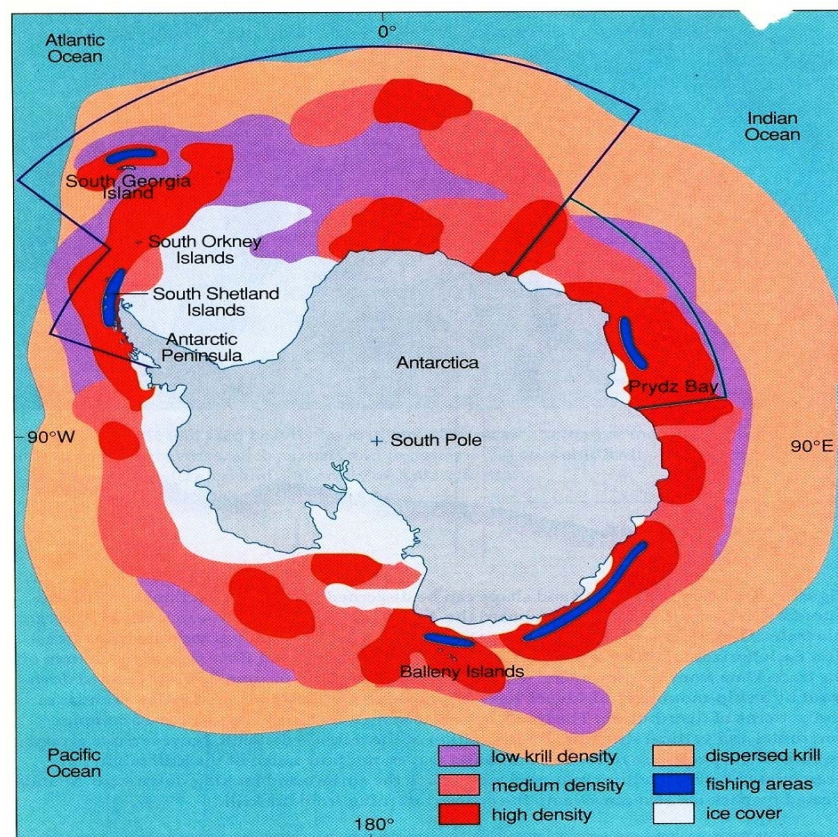
**Fig. 3** Conceptual view of krill stock density and spatial distribution of size classes along the Antarctic Peninsula (source: Siegel 2005:3)

Siegel (2005) also noted that juvenile krill primarily inhabit coastal waters around the Antarctic Peninsula while mature adults congregate to spawn in open ocean along the continental shelf break (Fig. 3). This is suggested to be a life history strategy to avoid competition for food between juveniles and adults while also preventing cannibalism on larval krill by adults (Siegel 2005).



Fig. 4 shows a map based on fishing data from the former Soviet Union fishing fleet. Fishing areas are comparatively small compared to the total distribution of krill and international precautionary limits apply to the krill fishery in the outlined areas (Nicol and de la Mare 1993).

The map also illustrates that coastal areas surrounding Antarctica appear to have the highest density krill swarms during the summer while further north krill are more dispersed (Nicol and de la Mare 1993).



**Fig.4** Summer distribution of krill around Antarctica based on Soviet Union fishing fleet data. Low density area catches less than 1 ton/hr, high density area catches were up to 30ton/hr (source: Nicol and de la Mare 1993:42)

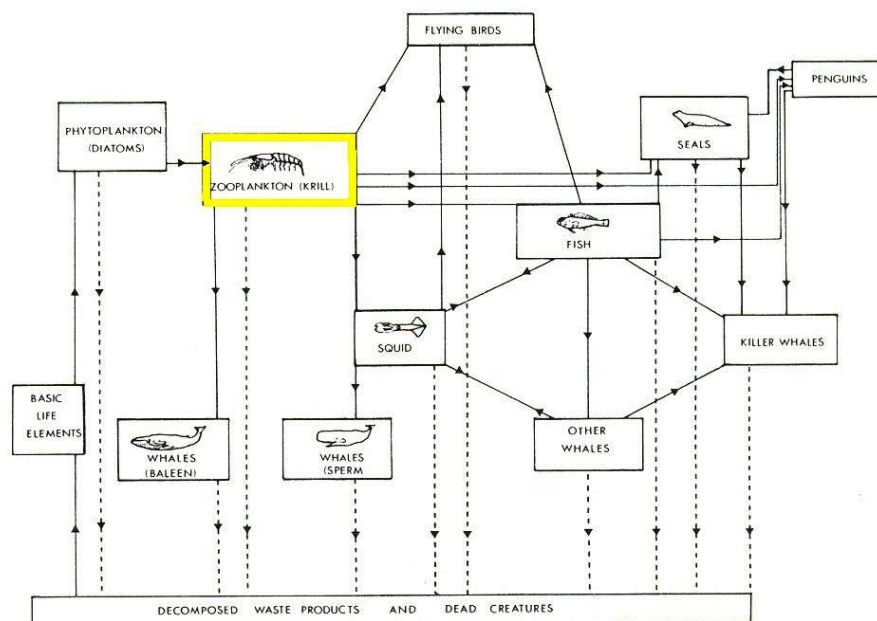
Seasonal differences in krill abundance between summer and winter are another area of interest among scientists, and there are several theories as to where the krill migrate to during the winter months. The ‘conveyor’ explanation is that krill may be retained by the pack ice over the winter and released again during spring (Siegel 2005). An alternative hypothesis to this suggests that during winter, krill migrate down the water

column to depths below 200 meters (Kawaguchi et al in Siegel 2005). This view is supported by Japanese trawl data obtained from the Scotia Sea (Taki et al in Siegel 2005). There are also diurnal variations in the vertical distribution of krill (Kirkwood 1982). Most krill rise from depth at night to feed on phytoplankton at the surface. This is thought to be a defence mechanism to minimise the risk of surface predation and potentially provide more mating opportunities while swarming (Kirkwood 1982). Differences in vertical migration also varied with season in proxy trawl data gathered by Taki et al (Siegel 2005).

Several studies have also identified that in late winter, krill concentrate beneath the sea ice to consume ice algae, which conforms to the gradual increase in krill density seen at the ice edge with the onset of spring (Siegel 2005).

## Trophic Significance of Krill

Krill occupy an important position in the trophic structure of the Southern Ocean food web, and directly or indirectly support populations of major Antarctic species (Fig. 5).



**Fig.5** The Antarctic marine food web illustrating trophic interactions between key species in the Southern Ocean. The position of krill is highlighted in yellow (source: Miller and Hampton 1989:3)

Human trophic effects on the krill population are not shown in Fig. 5, however harvesting of whales and seals by man to the brink of extinction has reduced predation

pressure on Antarctic Krill, and indirectly lead to an overall increase in biomass (Nicol and de la Mare 1993).

Krill are omnivorous and their diet changes according to the season (Kirkwood 1982). In summer when increased sunlight stimulates primary productivity, krill feed mostly on phytoplankton, conversely in winter when there is less available light limiting phytoplankton growth it is assumed that krill feeding alters or stops completely (Kirkwood 1982).

Pakhomov et al (1997) looked at feeding dynamics of *Euphausia superba* in the South Georgia region during the summer of 1994. In their study, it was found that total krill grazing impact on phytoplankton ranged from 10 to 59% of the total daily primary production. Grazing impact on microphytoplankton (>20 µm in size) was found to be much higher, sometimes eclipsing the level of daily microphytoplankton production (Pakhomov et al 1997).

Historical studies have used estimates of total primary production and subsequent consumption rates by krill in order to calculate krill productivity, but indirect estimates of krill productivity have also been formulated by examining krill consumption by predators (Miller and Hampton 1989).

Table 1. Krill Consumption by Predators

<b>Predator</b>	<b>Rate of Krill Consumption</b>
Whales	190 million tons year <sup>-1</sup>
Seals	64-130 million tons year <sup>-1</sup>
Squid	17 million tons year <sup>-1</sup>
Fish	10-100 million tons year <sup>-1</sup>
Seabirds	25 million tons year <sup>-1</sup>
Humans	288 546 tons year <sup>-1</sup> (1991-1992)

(Source: Miller and Hampton 1989:87-89)

Table 1 details the major consumers of krill biomass with the amount caught commercially by human fishing appearing insignificant when compared with the other estimated volumes being consumed. In 1991, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) decided to restrict the annual catch of Antarctic Krill to 1.5 million metric tons; however, annual catches of krill have never come close to the maximum allowable limit (Nicol and de la Mare 1993). The krill fishery peaked at 500,000 metric tons in the early 1980's but catches have been declining due to economic limitations (Nicol and de la Mare 1993).



## **Krill and the ‘Biological Carbon Pump’**

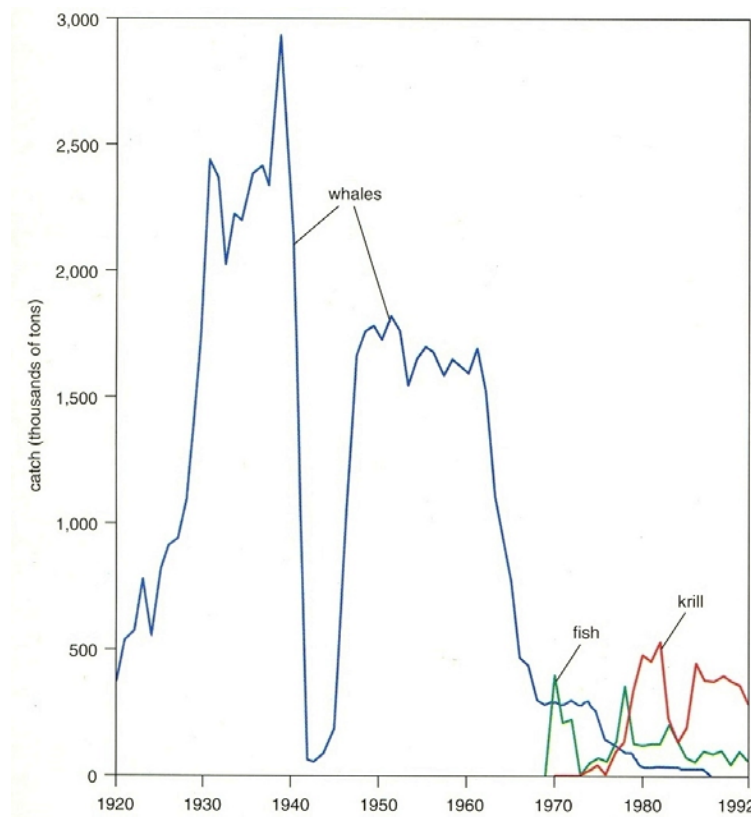
The ocean is the largest non-geological store of carbon (Gibson 1998). The Southern Ocean covers approximately 36 million km<sup>2</sup> and is a major sink for atmospheric carbon (Bathmann et al 2000). Krill play a key role in maintaining the ‘Biological Carbon Pump’ of atmospheric carbon (CO<sub>2</sub>) and coupled with other biological factors in the ocean, are an important element in carbon uptake and the cycling of nutrients within the ecosystem (Nicol and de la Mare 1993).

Photosynthesis by phytoplankton utilizes dissolved CO<sub>2</sub> to produce organic carbon as net primary productivity (Gibson 1998). Krill are the next step in the biological sequestration of carbon into the oceans and consume a large amount of heterotrophic carbon as phytoplankton (Pakhomov et al. 1997). As primary consumers, krill assimilate carbon during digestion, which is in turn cycled through the system when they are predated upon by secondary and tertiary consumers. At the bottom of this food web are the detritivores and bacteria, which feed on dead and decaying organic matter that settles on the seafloor. Due to the large biomass of krill, particulate organic matter (POM) in the form of faecal pellets and dead individuals form a significant food source for benthic detritivores (Gardner 2000). The POM falls as what is known as “marine snow” and is then broken down by benthic organisms and either buried as a carbon sink in the seafloor sediments or re- released into the water as mineral NCO<sub>3</sub> (Gardner 2000).

Analysis of faecal pellet production data estimated the daily carbon consumption of individual krill at up to 2.73 mg C.ind<sup>-1</sup>.day<sup>-1</sup> or 5% of total body carbon (Pakhomov et al. 1997). Not only do krill act as a large carbon sink while increasing their biomass but they also contribute to the sedimentation of carbon on the ocean floor in the form of particulate organic matter (POM) such as faecal pellets, dead individuals and moulted carapace shells (Gardner 2000).

## **Implications of Harvesting**

Impacts of harvesting Southern Ocean marine resources have been significant since the 19th century, as major Antarctic species were systematically hunted to near extinction (Nicol and de la Mare 1993). When seals became scarce, the focus moved to harvesting whales, which continued until the end of last century (Fig. 6). Whales only had a brief respite from hunting during World War 2 before continued harvesting led to many whale species becoming endangered too (Fig. 6).



**Fig.6** Graph illustrating progressive exploitation of Antarctic marine resources (source: Nicol and de la Mare 1993:40).

A decline in finfish catches preceded the beginning of the krill fishery in the mid-1970's (Fig. 6). The collapse of many other commercial fisheries has now forced fishing vessels to venture further south in search of untapped fishery resources. This has large implications for Antarctic krill and the functioning of the Southern Ocean Ecosystem. Russia and Japan were the first two countries to begin a krill fishery and krill harvest peaked in 1980-1981 with a catch of over half a million tons (Nicol and de la Mare 1993).

There is now believed to be a large 'surplus' of krill as a result of removing most of the major predators from the Southern Ocean ecosystem (Nicol and de la Mare 1993). Direct harvesting of krill however, has remained relatively small scale due to the high levels of processing required, the lack of markets to buy krill and the increasing cost of fuel making it largely uneconomic to take trawlers to Antarctic waters (Nicol and de la Mare 1993).

To mitigate potential adverse effects of krill harvesting the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) have imposed a pre-

emptive strategy to manage krill. Currently they have in place an annual limit of 1.5million tons of krill for the South Atlantic sector where most Antarctic krill is caught (Nicol and de la Mare 1993). CCAMLR is also undertaking an ecosystem-monitoring programme to look at possible effects of krill harvesting on breeding populations of seals and birds adjacent to the major krill fishing grounds.

## **Conclusion**

Since the early 'Discovery' studies of the 1920's, there has been numerous research conducted into the biology and physiology of Antarctic krill. During this time, technological advances have enabled better estimates of krill biomass to be measured using remote sensing, hydro-acoustic surveys and trawl data, while laboratories are now equipped to maintain krill experiments for successive years using sophisticated artificial environments. These experiments have developed our knowledge and reinforced the trophic significance of krill as a primary consumer in the Southern Ocean ecosystem and as a food source for other species (including ourselves). Krill is also a key organism in the cycling of carbon within the oceanic system, which is significant in terms of a possible regulating mechanism for global warming as a result of greenhouse gas increases in the atmosphere. Despite the many research projects currently focussing on Antarctic krill, there are still gaps in our knowledge of this cryptic species. We know that krill occupy a key role in the Southern Ocean ecosystem and cycling of carbon and we are aware of the trophic significance of krill, by the number of other species that utilize krill as a food source but little is known about the response of krill populations to increasing fishing pressure.

Up until now, there has been minimal human pressure on krill populations; that is likely to change in the next few years as commercial interests seek out new potential fisheries and develop new harvesting and processing technology. If any lessons are to be learned from past catastrophic marine resource use it is that sustainable management practices need to be employed early to avoid population crashes such as in the whale and seal populations of the Southern Ocean. As anthropogenic pressure increases on krill populations, the current knowledge will need to be built upon and utilized by decision-makers to assist organisations such as CCAMLR to manage the krill population sustainably while maintaining species diversity across all trophic levels of the Southern Ocean Ecosystem.

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